Biodivers Conserv (2017) 26:717–734
DOI 10.1007/s10531-016-1269-5

ORIGINAL PAPER

# 17 years of grassland management leads to parallel local and regional biodiversity shifts among a wide range of taxonomic groups

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Received: 28 June 2016 / Revised: 22 October 2016 / Accepted: 25 October 2016 /
Published online: 9 December 2016


**Abstract** Conservation management is expected to increase local biodiversity, but uniform management may lead to biotic homogenization and diversity losses at the regional scale. We evaluated the effects of renewed grazing and cutting management carried out across a whole region, on the diversity of plants and seven arthropod groups. Changes in occurrence over 17 years of intensive calcareous grassland management were analysed at

Communicated by Jens Wolfgang Dauber.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10531-016-1269-5) contains supplementary material, which is available to authorized users.

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the species level, which gave insight into the exact species contributing to regional homogenization or differentiation. Reponses were compared between species differing in habitat affinity, dispersal ability, food specialisation and trophic level. Local species richness increased over the sampling period for true bugs and millipedes, while carabid beetles and weevils declined in local species richness. Species richness remained unchanged for plants, woodlice, ants and spiders. Regional diversity and compositional variation generally followed local patterns. Diversity shifts were only to a limited extent explained by species' habitat affinity, dispersal ability, trophic level and food specialisation. We conclude that implementation of relatively uniform conservation management across a region did not lead to uniform changes in local species composition. This is an encouraging result for conservation managers, as it shows that there is not necessarily a conflict of interest between local and regional conservation goals. Our study also demonstrates that shifts in diversity patterns differ markedly between taxonomic groups. Single traits provide only limited understanding of these differences. This highlights the need for a wide taxonomic scope when evaluating conservation management and demonstrates the need to understand the mechanisms underlying occurrence shifts.

**Keywords** Beta-diversity · Insects · Arthropods · Plants · Conservation management · Trait

## Introduction

Semi-natural habitats have suffered large diversity losses due to land use change, abandonment, eutrophication and fragmentation (Millenium Ecosystem Assessment 2005). This has led to regional diversity losses, both through decreased local species richness and through biotic homogenization (McKinney and Lockwood 1999, 2001; Ekroos et al. 2010). Biotic homogenization is the non-random loss and gain of species leading to reduced compositional variation (β-diversity) among communities, usually caused by a loss of rare specialist species and an increase in common generalist species (McKinney and Lockwood 1999; Olden et al. 2004). The resulting genetic, taxonomic and functional impoverishment is viewed as a major threat to biodiversity (Olden et al. 2004; Mouillot et al. 2013). Biotic homogenization has been demonstrated to occur across nearly all taxonomic groups, spatial scales and grain sizes (Baiser et al. 2012). This makes it paramount to understand how biotic homogenization can be counteracted at each of these scales.

At the site scale, unimproved semi-natural grasslands, have often suffered biodiversity losses due to abandonment of traditional management practices, which leads to grass and

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shrub encroachment. Such losses can potentially be restored through renewed conservation management like grazing or mowing (Bobbink and Willems 1993; Hobbs and Norton 1996; Pykälä 2003; Pöyry et al. 2004). However, the effect of such management practices on regional biodiversity and the compositional variation among sites has yet received little attention. Theoretically, conservation and restoration management carried out across multiple sites within a region can have multiple effects on regional diversity patterns (Rooney et al. 2007). If the management strengthens inherent environmental differences between sites, different specialist species will be attracted to each site, increasing regional biodiversity and the compositional variation among sites (scenario A in Fig. 1). However, if all sites change in the same way, because they are all subject to the same management regime, compositional variation among sites may decrease, leading to increased homogenization (Konvicka et al. 2008; Verberk et al. 2010) and decreased regional diversity (scenario B in Fig. 1). If local diversity does not increase after renewed management, the compositional variation among sites may still increase, e.g. due to a reduction in generalist species that occur across all sites prior to management (scenario C in Fig. 1). Finally, management can fail to increase both local and regional diversity (scenario D in Fig. 1). This is, for example, the case when characteristic species are unable to return due to dispersal limitations (Donath et al. 2003; Ozinga et al. 2005; Woodcock et al. 2010a). Conservation management may thus have contrasting effects on local and regional diversity patterns and may lead to increased biotic differentiation or conversely, amplify biotic homogenization.

In addition to potential discrepancies between responses of local and regional diversity to conservation management, there may also be differences between taxonomic groups. It

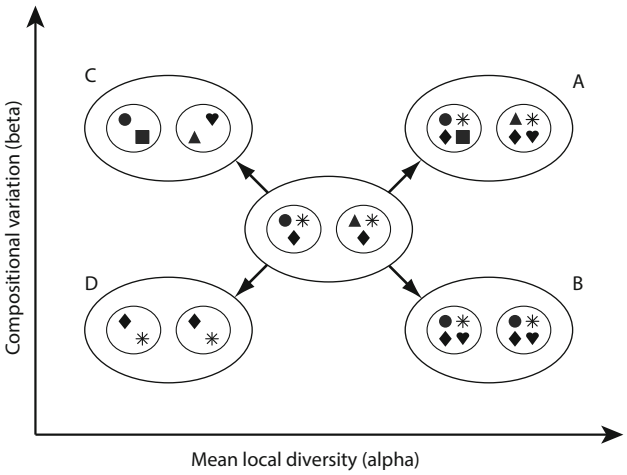


**Fig. 1** Potential effects of conservation management on local diversity (α) and the compositional variation among sites (β-diversity). Each situation (*A–D*) depicts two hypothetical sites within a region, with different symbols depicting different species. From the initial situation (in the *middle*), management can lead to: *A* Increased species richness and compositional variation, e.g. by strengthening inherent environmental differences between sites, which attract different species to different sites; *B* Increased species richness, but decreased compositional variation, caused by all sites changing in the same way; *C* Decreased species richness, but increased compositional variation, e.g. through a reduction in common (generalist) species, while still strengthening inherent environmental differences between sites; *D* Decreased species richness and compositional variation, due to negative side effects (e.g. overgrazing) and/or the inability of species to recolonize restored sites due to dispersal limitations

has repeatedly been demonstrated that the response of species to conservation management differs markedly among taxonomic groups (Kruess and Tscharntke 2002; Oertli et al. 2005; van Klink et al. 2015). Such taxonomical variation has been linked to various species' characteristics, including dispersal ability, habitat and food specialization and trophic level. Species with a well-developed dispersal ability colonise restored habitat at a higher rate than poorly dispersing species (Ozinga et al. 2005; Lambeets et al. 2009; Öckinger et al. 2010; Woodcock et al. 2010a, 2012). Characteristic species and food specialists are generally more vulnerable to habitat degradation (Römermann et al. 2008; Öckinger et al. 2010), but are also expected to respond more positively to renewed management than non-characteristic and food generalist species, because habitat conditions improve most for them. Finally, a species' trophic position modulates its sensitivity to processes operating at larger spatial scales (Holt et al. 1999; Vanbergen et al. 2010; van Noordwijk et al. 2015), making higher trophic levels more vulnerable to habitat fragmentation (Purtauf et al. 2005; Krauss et al. 2010; van Noordwijk et al. 2015). These species characteristics vary between species and, even more so, between taxonomic groups. So far, remarkably few studies have simultaneously investigated changes in regional diversity patterns for more than one taxonomic group (Baiser et al. 2012, but see Shaw et al. 2010).

In this study we investigate shifts in local and regional diversity patterns over 17 years of conservation management. We use a unique dataset of presence/absence data for plants and seven arthropod groups in eight calcareous grasslands within a single region. All study sites are similar in geology and climate and suffered from agricultural intensification, eutrophication and abandonment of traditional farming practices over the course of the twentieth century (Willems 2001). This resulted in strong declines in species richness, especially among initially rare, characteristic plant and arthropod species (WallisDeVries et al. 2002; Smits 2010). This, in turn, led to biotic homogenization (Polus et al. 2007; Smits 2010; Ekroos et al. 2010). To mitigate these negative effects of land-use change and eutrophication, conservation management was introduced in the 1980ies. In all sites, conservation management consisted of annual intensive grazing and/or mowing in autumn, although details of management execution differed between sites and years.

Our dataset covers all calcareous grassland sites within the Dutch region of South-Limburg that were of reasonable conservation value and had a surface area of more than 1 ha. in 1988. Combined with the fact that conservation management of a similar type was introduced in all sites around the same time, this makes our dataset uniquely suitable to investigate the effects of conservation actions on local and regional diversity patterns. Using a species-based approach we specifically investigate (1) whether 17 years of conservation management have led to increased local biodiversity, (2) whether this has led to increased regional biodiversity and increased biotic differentiation, or conversely, biotic homogenization, (3) whether shifts in local and regional diversity differ between taxonomic groups and (4) whether simple species characteristics such as dispersal ability, trophic level and the degree of food specialisation explain interspecific variation in occurrence shifts.

## Methods

### Study region

The study was conducted in eight calcareous grasslands in South-Limburg, the Netherlands (see Appendix S1), which comprises all calcareous grassland sites within this region that were of reasonable conservation value and had a surface area of more than 1 ha. in 1988. South-Limburg has an undulating hilly landscape up to 323 m above sea level. The main soil type is loess with calcareous deposits occurring close to the surface on some of the slopes. Most of the landscape is used for agricultural production, with forest and semi-natural grassland remnants predominantly limited to the steeper slopes (Willems 2001). The study sites range in surface area from one to five hectares and are all located on slopes with an eastern, southern, or western aspect. They were originally grazed by sheep until the early twentieth century and were subsequently abandoned or irregularly managed for several decades. One site (Wrakelberg) was partially used as an arable field for a short period in the 1960s, but was quickly restored to calcareous grassland through natural regeneration. The top section of the site, which was never ploughed, acted as a seed source. All other sites have a continuous history as calcareous grassland. Regular management for nature conservation purposes was introduced in all sites between 1978 and 1990 and consisted of annual intensive sheep grazing and/or large scale mechanical mowing (Willems 2001). All sites were intensively managed in autumn, resulting in a homogeneous, short sward over winter. Some sites were additionally (partially) grazed for a short period in summer. The management method, timing and intensity remained largely unchanged throughout the study period, although management details (exact stocking density, rotation scheme within sites, exact timing, etc.) fluctuated from year to year.

### Data collection

Arthropods were sampled by means of standardised pitfall sampling in 1988, shortly after or around the time of renewed regular conservation management and again in 2005 or 2006 (referred to as 2005). All true bugs (Heteroptera), carabid beetles (Coleoptera, Carabidae), weevils (Coleoptera, Curculionidae), ants (Hymenoptera, Formicidae), spiders (Araneae), woodlice (Isopoda) and millipedes (Diplopoda) were identified to species level (see Appendix S2 for more details, including nomenclature). Because of the applied pitfall sampling, our data represent the ground dwelling proportion of the sampled species groups only, rather than a complete overview of species. Vegetation data were taken from the Dutch Vegetation Database (Schaminée et al. 2012) covering the periods 1970-1992 (referred to as 1988) and 1997–2007 (referred to as 2005). Details on the number and size of relevees are given in Appendix S2. Where sampling efforts differed between the two sampling periods, we took random subsamples to obtain a balanced dataset (see Appendix S2).

Using published literature, we compiled a dataset on species' trophic level (primary producers, first order consumers, predators and detritivores), habitat affinity (characteristic versus non characteristic species for calcareous grasslands), food specialisation (monophagous, oligophagous and generalist) and dispersal ability (good, poor and unknown). All literature sources and trait attributes per species are listed in Appendix S3. Species which shift in trophic level during their life-cycle (notably a few carabid species) were classified according to their larval characteristics, because larvae are generally less mobile and more

vulnerable to adverse microclimatic conditions and food shortages than adults (Thiele 1977; Bourn and Thomas 2002; Fartmann and Hermann 2006). Habitat affinity was classified as 'characteristic' if species mainly occur in dry, nutrient poor grasslands and as 'non-characteristic' if they are (also) common in wet or nutrient rich grasslands or woodlands. Good and poor dispersal ability were defined respectively as presence or absence of long distance dispersal strategies (LDD) in plants and as presence or absence of individuals capable of active flight for carabid beetles, weevils and true bugs. For ants, dispersal ability was judged from their life history strategy (van Noordwijk et al. 2012a), with species mainly founding new nests through social-parasitism or nest-splitting defined as poor dispersers. For spiders, dispersal ability was categorized based on behaviour traits, including ballooning. For millipedes and woodlice body size was used as a substitute for dispersal ability. Body-size is not an ideal proxy for dispersal ability, but there is evidence that it is strongly related to dispersal (Stevens et al. 2014). More accurate estimates of actual dispersal ability were not available for millipedes. For woodlice, we could have used unpublished measurements of walking speed, but we decided against this, because it is unclear how the proxy individual walking speed relates to species level dispersal ability. For all taxonomic groups, a third category was made, containing species for which the dispersal ability is unknown.

## Statistical analysis

Statistical analyses were performed per taxonomic group. Results were structured according to the overall trophic level of the taxonomic group, but for all species-based analysis the actual trophic level of each species was used (e.g. carabid beetles were included in tables and figures as predators, but in individual analyses, granivorous species were labelled as first order consumers). For vascular plants all analyses were performed for each of the replicate datasets (see Appendix S2) and results were averaged. First, the mean species richness per site and sampling period was calculated (α-diversity) as well as the total number of species for each sampling period (γ-diversity). Changes in α-diversity per site were calculated using the formula: $\Delta\alpha = \frac{\alpha[new]-\alpha[old]}{\alpha[new]+\alpha[old]}$. This means that $\Delta\alpha$ can range from $-1$ to 1 and that negative values represent a decrease in species richness, while positive values represent an increase. Changes in γ-diversity were calculated analogously. Generalized estimation equations were used to test for significant changes in α-diversity (dependent variable) over time (independent variable), using a Poisson distribution and sites as the grouping variable. A two-sided Pearson correlation test was used to establish whether changes in α- and γ-diversity were correlated across taxonomic groups. To visualise species-turnover rates, the fraction of occupied sites in 1988 was plotted against the fraction of occupied sites in 2005 for each species.

The compositional variation among sites (β-diversity) was quantified with a model-based multiple-site metric *D*. This metric was developed by Baeten et al. (2014) and is in line with new model-based thinking for the analysis of community data (Warton et al. 2015). The metric is derived from a species-level measure of heterogeneity of occurrence ($D_i$), summed across the species. *D* is low if the community dataset has many species that are either rare (absent in most sites) or prevalent (present in most sites). Such species do not contribute much to the compositional variation among communities. Homogenization occurs if many species decrease their heterogeneity of occurrence over time ($\Delta D_i < 0$, so their sum $\Delta D < 0$), i.e., rare species becoming rarer or prevalent species becoming more prevalent. Differentiation occurs when most species increase their heterogeneity

($\Delta D_i > 0$). This method was chosen instead of classical diversity metrics, such as the Shannon diversity index, because it is not biased by differences in alpha diversity (Baeten et al. 2014) and is based on the individual species responses that were observed, rather than summary statistics derived from those observations. This allows to separate homogenizing effects caused by species becoming prevalent from those caused by species becoming very rare. In addition, it allows to analyse the effects of species' traits without the need to average categorical trait attributes, making this method particularly suitable for the questions addressed here.

The significance of species-level and community-level homogenization or differentiation was tested with a permutation test (999 permutations). Permutational analysis of variance (PERMANOVA, 999 permutations) was also used to test for effects of the traits trophic level, dispersal ability, habitat affinity and food specialism (independent variables) on the individual species responses $\Delta D_i$ and change in occupancy over time (fraction occupied sites 1988 minus fraction occupied sites 2005). Only main traits and two-way interactions were included in this analysis and preliminary tests were performed to determine the order in which traits should be added to the model (most influential traits were added first). All analyses were carried out in R (R Core Team 2013) using the packages Geepack (Højsgaard et al. 2006) and Vegan (Oksanen et al. 2013).

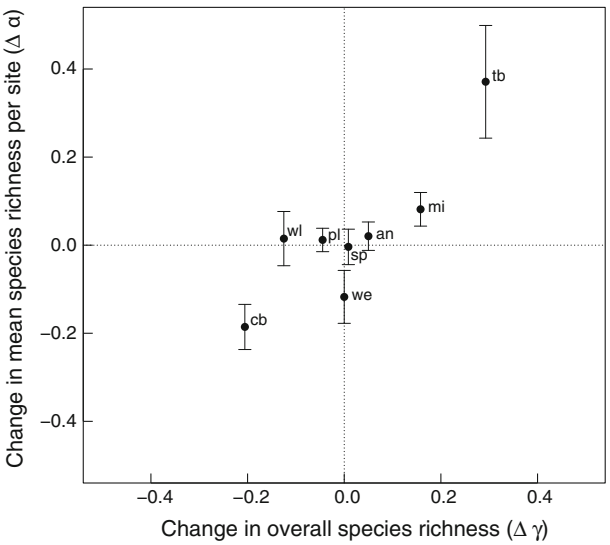


**Fig. 2** Change in mean species richness per site between 1988 and 2005 (±1.0 SE) against the change in overall species richness over the same period per taxonomic group (*an* ants, *cb* carabid beetles, *mi* millipedes, *pl* vascular plants, *sp* spiders, *tb* true bugs, *we* weevils, *wl* woodlice). Positive changes indicate an increase in richness, negative values represent a decrease

**Table 1** Change in mean species richness per site between 1988 and 2005 (Δ α-diversity), p value for the generalized estimation equation (GEE) testing for significant changes in α-diversity and change in overall species richness (Δ γ-diversity) per taxonomic group

| Trophic level | Taxonomic group | Δ α-diversity | p value | Δ γ-diversity |
|---|---|---|---|---|
| Primary producers | Plants | 0.012 | 0.588 | −0.045 |
| Macrodetritivores | Woodlice | 0.015 | 0.785 | −0.125 |
| | **Millipedes** | **0.081** | **0.025** | 0.157 |
| 1st order consumers | **True bugs** | **0.371** | **0.008** | 0.293 |
| | **Weevils** | **−0.117** | **0.011** | 0.000 |
| Predators | **Carabid beetles** | **−0.186** | **<0.001** | −0.206 |
| | Spiders | −0.004 | 0.922 | 0.009 |
| | Ants | 0.020 | 0.508 | 0.050 |

Groups showing a significant change in α-diversity ($p < 0.05$) are bold

## Results

### Local diversity

We found no consistent change in local species richness (α-diversity) over 17 years of calcareous grassland management (Fig. 2). Carabid beetles and weevils decreased in α-diversity, while true bugs and millipedes showed an increase in local species richness (Table 1). Local richness of plants, spiders, ants and woodlice did not change over time.

### Regional diversity and compositional variation

Regional diversity (γ-diversity) patterns generally followed local patterns (Pearson $R^2 = 0.75$; df = 6; $p = 0.006$), with carabid beetles decreasing in γ-diversity, while γ-diversity increased for true bugs and millipedes (see Table 1). Few species had identical relative frequencies in both sampling periods (along diagonal in Fig. 3). This implies that considerable species turn-over occurred over time for all groups. This could cause increased biotic homogenization or differentiation, independent of local species richness changes. However, significant changes in compositional variation among sites was only found for two taxonomic groups. Carabid beetle communities became increasingly homogenized over time (Table 2), mainly because many initially rare species became rarer (Fig. 3). In contrast, millipede communities became increasingly differentiated (Table 2), due to some rare species becoming more prevalent as well as some common species becoming rarer (Fig. 3).

### Species characteristics

Shifts in local and regional diversity were not consistent within trophic levels (see Fig. 3). For example, opposing diversity shifts were found for true bugs and weevils, the two first order consumer groups included in our study. Also, none of the species characteristics included in our analysis consistently explained species replacement patterns across taxonomic groups (see Appendix S4). However, within taxonomic groups, the tested species characteristics did explain some of the variation in species turnover. Habitat affinity was

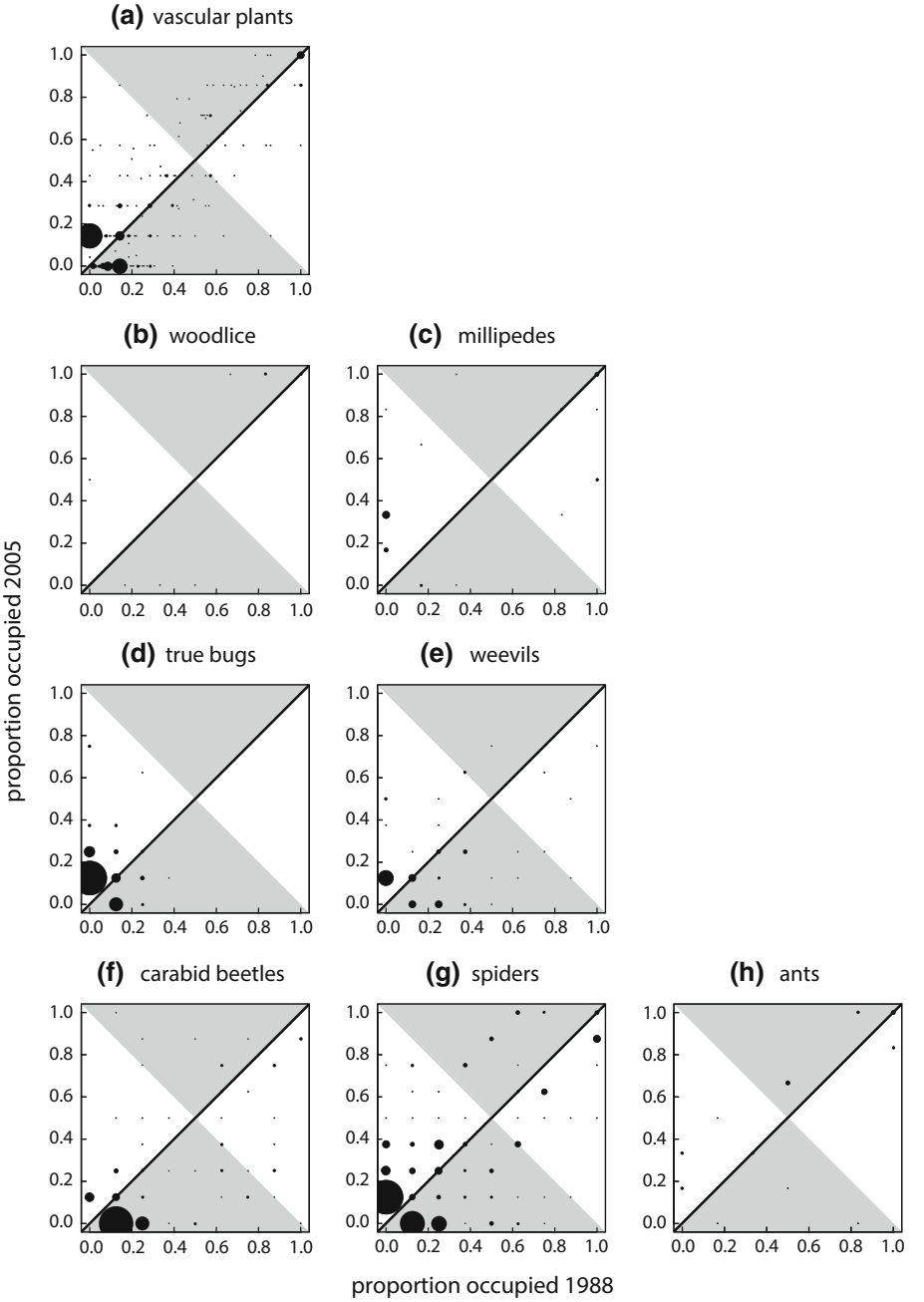


**Fig. 3** Proportion of occupied sites in 2005 versus 1988 for each species per taxonomic group ordered by trophic level. Overlapping species are represented as larger circles. The *diagonal line* represents no change in the proportion of occupied sites between the sampling periods. The *area* below this *line* represent a decrease in occurrence, the *area* above represents an increase. Species with frequency changes that fall in the *upper* and *lower triangles* (*grey*) cause biotic homogenization (rare becoming rarer or prevalent becoming more prevalent), species in the white triangles cause increased differentiation

**Table 2** Results of the delta deviance analyses per taxonomic group

| Trophic level | Taxonomic group | n sites | n species | $\Delta D$ | p |
|---|---|---|---|---|---|
| Primary producers | Plants | 7 | 223 | −97.51 | 0.447 |
| Macrodetritivores | Woodlice | 6 | 10 | −31.50 | 0.119 |
| | **Millipedes** | **6** | **25** | **60.23** | **0.030** |
| 1st order consumers | True bugs | 8 | 64 | 183.69 | 0.061 |
| | Weevils | 8 | 54 | −16.04 | 0.625 |
| Predators | **Carabid beetles** | **8** | **91** | **−199.89** | **0.029** |
| | Spiders | 8 | 151 | 1.309 | 0.988 |
| | Ants | 6 | 23 | 13.24 | 0.612 |

Significant results ($p < 0.05$) are given in bold and represent overall biotic homogenization for negative values of delta deviance and overall differentiation for positive values of delta deviance

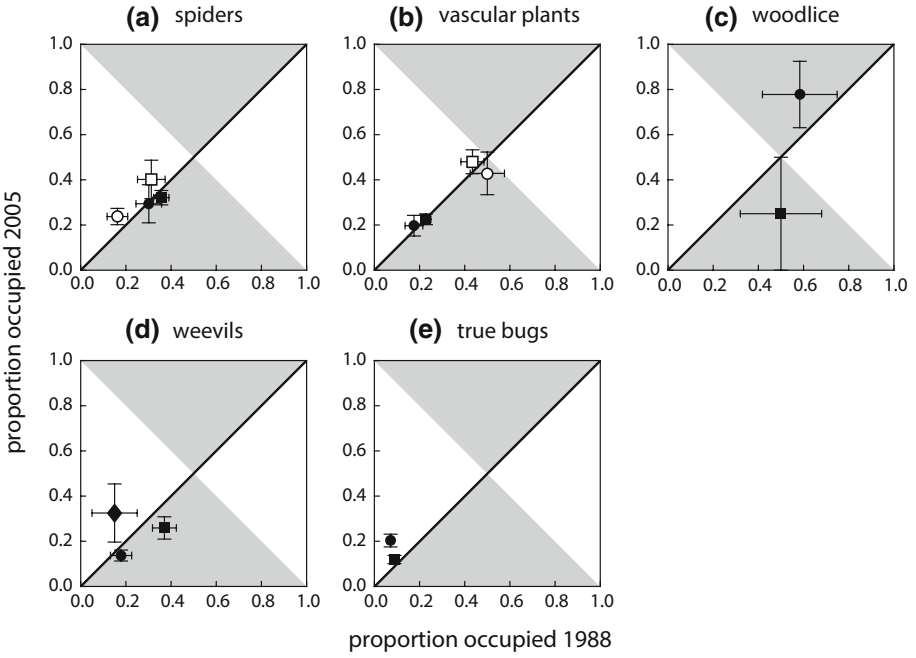


**Fig. 4** Mean proportion of occupied sites in 2005 versus 1988 (±1.0 SE) for species from different trait categories, with *white symbols* depicting habitat specialists and *black symbols* depicting habitat generalist. Only the five taxonomic groups showing significant trait effects are shown. **a** Spiders classified as habitat specialists and habitat generalists with good (*squares)* and poor (*circles*) dispersal ability. **b** Vascular plants classified as habitat specialists and habitat generalists with good (*squares*) and poor (*circles*) dispersal ability. **c** Woodlice larger (*circle*) and smaller (*square*) than 10.5 mm in body size. **d** Weevils classified as polyphagous (*square*), oligophagous (*circle*) and monophagous (*diamond*). **e** true bugs classified as herbivorous (*circle*) and carnivorous (*square*). The *diagonal line* represents no change in the proportion of occupied sites between the sampling periods. The *area* below this *line* represent a decrease in occurrence, the *area* above represents an increase. The *upper* and *lower triangles* (*grey*) are associated with biotic homogenization, the *left* and *right triangles* (*white*) are associated with increased differentiation between sites

significantly related to the decrease or increase of spiders (Permanova: df = 1, 144; $R^2 = 0.036$; p = 0.026), with characteristic species increasing more than others (Fig. 4a). The interaction between habitat affinity and dispersal ability significantly explained which spider species contributed to overall homogenization or differentiation (Permanova: df = 1, 144; $R^2 = 0.044$; p = 0.011). Good dispersers initially occurred in more sites than poor dispersers. For the initially rare characteristic species with poor dispersal ability an increase in occurrence led to an increase in compositional variation. For the initially more widespread characteristic species with good dispersal ability the same increase in occupancy had no effect on the compositional variation between sites. Conversely, the decline of non-characteristic species with poor dispersal ability led to homogenization, as initially rare species became rarer. The same decline had no effect on the compositional variation among sites for non-characteristic species with good dispersal abilities, which were initially more widespread (Fig. 4a). For plants there was a trend towards interaction (Permanova: df = 1, 219; $R^2 = 0.018$; p = 0.060) between habitat affinity and dispersal ability on the decrease or increase in occurrence (Fig. 4b). Characteristic species tended to increase more than other species, but only if they exhibit long distance dispersal strategies. Poorly dispersing characteristic species tended to decrease in occurrence, even more so than non-characteristic species. For woodlice, body size had a significant effect on the change in occurrence over time (Permanova: df = 1, 6; $R^2 = 0.70$; p = 0.003). Large woodlice increased in occurrence, while small woodlice decreased over time (Fig. 4c).

For weevils, a significant difference in occurrence change was found between food specialists and generalists (Permanova: df = 1, 47; $R^2 = 0.089$; P = 0.024). Monophagous species on average increased in occurrence, while oligophagous and polyphagous species tended to decrease in occurrence over time (Fig. 4d). With respect to trophic level, no significant effects were found within taxonomic groups, although for true bugs there was a trend towards phytophagous species increasing more than zoophagous species (Permanova: df = 1, 50; $R^2 = 0.062$; p = 0.057, Fig. 4e).

## Discussion

Conservation management has been an effective tool to counteract diversity loss at local scales (Bobbink and Willems 1993; Hobbs and Norton 1996; Pykälä 2003; Pöyry et al. 2004), but its effects on regional biodiversity remain little studied (but see Doxa et al. 2012). Using a unique dataset of species presence/absence data before and after 17 years of conservation management for a wide range of taxonomic groups, we evaluated the effects of conservation actions on both local and regional diversity patterns. Shifts in local and regional biodiversity were highly correlated, indicating that there was no discrepancy between local and regional conservation success. However, diversity shifts differed markedly between taxonomic groups, with some taxa decreasing in local and regional diversity, while others became more diverse over time.

### Local diversity shifts

Over 17 years of conservation management, local species richness changed significantly for half of the eight investigated taxonomic groups, with increased richness and decreased richness each occurring in two taxonomic groups. Conservation management in Dutch calcareous grasslands has thus not resulted in the anticipated increase in local species

richness across taxonomic groups. A lack of response to conservation measures is often attributed to slow recovery of plant and arthropod communities (Huxel and Hastings 1999; Woodcock et al. 2012). However, considering the long time-span of our study (17 years), we would expect to have picked up even relatively slow responses. The lack of recovery may, in part, reflect a lack of source populations in the landscape. Our sampling sites comprised all calcareous grassland sites of reasonable quality and more than 1 ha. in size within the landscape. Species not present in any of these sites may have been completely absent from the landscape and therefore unable to recolonize restored locations. The large variation in species composition between sites, however, indicates that this is not the only explanation. In the absence of control sites that did not receive conservation management, we cannot automatically attribute observed shifts in diversity patterns (or the lack thereof) to the implemented conservation management. Other factors that have affected the study sites simultaneously, e.g. ongoing agricultural intensification in the wider landscape, may have equally contributed to observed patterns, or may have cancelled out positive effects of conservation management. Given the generally negative trend of (specialist) species in northwestern European agricultural landscapes (Green et al. 2005; Kleijn et al. 2009; Potts et al. 2010) and the considerable impact of the implemented conservation management on vegetation structure and microclimate (Willems 2001; van Noordwijk et al. 2012a, b) it is likely that local species richness would have declined in the absence of conservation management. The fact that local species richness remained stable or increased for six out of eight taxonomic groups, could therefore be seen as (moderate) conservation success. For the two remaining groups, carabid beetles and weevils, the implemented conservation management has not prevented local diversity loss. The management may even have directly contributed to their decline, for example by causing increased mortality, food shortages or unfavourable microclimatic conditions (van Klink et al. 2015).

### Regional diversity and compositional variation

Local diversity shifts were strongly correlated to regional diversity shifts and were generally paralleled by shifts in compositional variation. We found increased community differentiation in millipedes, which increased in local species richness, while carabid beetles, which decreased in local species richness, became increasingly homogenized. This implies that observed changes in compositional variation were caused predominantly by changes in local species richness, rather than replacement of species (Baeten et al. 2014). We found no evidence for increased biotic homogenization resulting from a limited set of species profiting from the creation of similar environmental conditions across sites. This is an encouraging result for site managers as it shows that there is not necessarily a conflict of interest between local and regional conservation goals. Introducing similar conservation management across sites thus does not necessarily compromise regional biodiversity conservation by leading to sites becoming more similar in species composition.

### Differences between taxonomic groups

In our study, we observed both increases and decreases in local and regional biodiversity over 17 years of conservation management, depending on the taxonomic group under study. Relatively few studies have simultaneously investigated biotic homogenization patterns (Devin et al. 2005; Shaw et al. 2010) or the effects of conservation management (Kruess and Tscharntke 2002; Oertli et al. 2005) on more than one taxonomic group. Studies that do have a wide taxonomic scope, generally report differential responses

between taxonomic groups (Kruess and Tscharntke 2002; Devin et al. 2005; Oertli et al. 2005; Shaw et al. 2010), in line with our results. The reason for this variation in response between taxonomic groups is that species' distributions are affected by many different factors, including habitat fragmentation, regional land use, (micro)climatic conditions, biomass production and vegetation structure (Morris 2000; Sala 2000). The relative importance of each of these factors differs among taxonomic groups (Dormann et al. 2007). In addition, taxa also differ in their response to conservation management itself (van Klink et al. 2015). The eight taxonomic groups we investigated differ in many respects, including dispersal ability, trophic position, body plan and development pathway, which all play a role in determining species' responses to their environment (Verberk et al. 2008, 2013). We have not formally tested which factors explain the differences in diversity shifts between taxonomic groups, because there are more potential factors than the number of taxonomic groups in our study, which leaves insufficient statistical power for formal testing. However, in our highly fragmented study system, dispersal ability is likely to play a role. Fragmentation has repeatedly been demonstrated to hamper restoration of plant communities (Ozinga et al. 2005; Smits 2010), poorly dispersing beetles (Woodcock et al. 2010b) and ants (van Noordwijk et al. 2012a). This potentially explains why these groups did not increase in local and regional diversity in our study. True bugs, which showed the largest increase in richness over the study period, are generally better dispersers and have been shown previously to respond strongly to site conditions and not landscape factors (Kőrösi et al. 2012). Interestingly, the well-developed dispersal ability of many true bug species did not lead to increased biotic homogenization. In fact, no single true bug species was present in all study sites. This implies that either habitat characteristics differed between restored sites (causing species sorting), or that distances between sites were too large to ensure colonization of all sites, even for relatively good dispersers.

Contrary to our expectations, differences in trophic position did not seem to play a direct role in determining the response of taxonomic groups. Predominantly predatory groups showed negative (carabid beetle) and neutral (spiders and ants) changes in local biodiversity, while first order consumers responded positively (true bugs) and negatively (weevils). Interestingly, within both first order consumers and predators, the strongest decrease in diversity was found for holometabolous taxonomic groups (carabid beetles and weevils), while hemimetabolous groups responded more positively (true bugs and spiders). Holometabolous species generally have a more strongly synchronised life-cycle and their immature stages are less mobile and need different environmental conditions than the adult stages. This makes holometabolous species particularly sensitive to management timing, intensity and scale (van Noordwijk et al. 2012b; van Klink et al. 2015), indicating that too intensive management may have hampered restoration of carabid beetle and weevil communities.

It should be noted here that our study design, with only two sampling periods, makes it impossible to conclude unequivocally whether observed diversity changes represent ongoing shifts or mere year to year fluctuations. For example, carabid beetles are known to exhibit considerable annual population fluctuations (Baars and Van Dijk 1984; den Boer 1985, 1990; Brooks et al. 2012), presenting an alternative explanation for their observed decline in local and regional diversity. However, even if the observed diversity decline for carabid beetles is caused by annual population fluctuations rather than a decreasing trend, there is still reason for concern. The small size of individual sites (<5 ha.) and the large distance between sites, make species with large population fluctuations especially prone to local extinction (Henle et al. 2004; van Noordwijk et al. 2015).

## Species characteristics

In addition to the variation in responses between taxonomic groups, species within each group also differ in life-history, and hence in vulnerability to all the different factors affecting biodiversity (Stearns 1976; Southwood 1977). This causes a multitude of responses within each group, which are likely to cancel each other out and obscure overall patterns. Analyzing species' traits may help to disentangle such contrasting effects and our species-level analysis provides a unique opportunity to investigate consistent trait patterns. Conservation management is primarily aimed at improving conditions for characteristic species. A greater increase in characteristic calcareous grassland species, compared to habitat generalists, was indeed found for spiders. The fact that the replacement of non-characteristic spiders by characteristic species did not result in overall changes in compositional variation among sites, means that replacement was independent of the initial occurrence. Indeed, if both rare and prevalent characteristic species increase over time, there is no net-effect on the compositional variation. For weevils we found an effect of food type specialization with food specialists like *Sibinia pyrrhodactyla*, *Strophosoma fulvicorne*, *Trachyphloeus alternans*, *Trichosirocalus troglodytes* and *Tychius squamulatus* increasing more in occupancy than food generalists. This implies that conditions generally improved for these food specialists, which all feed on forbs that are well adapted to dry, nutrient poor conditions (*Spergula arvensis, Calluna vulgaris, Helianthemum nummularium, Plantago lanceolata* and *Lotus corniculatus*). The lack of increase in habitat- and food specialists in other groups (spiders, true bugs and carabid beetles) indicates that either conditions for specialists did not improve (at least not more so than for habitat generalists) or that specialists did not reach improved sites because of dispersal barriers. Our trait analysis revealed some evidence, albeit weak, for the existence of such dispersal barriers. The significant interaction between habitat affinity and dispersal ability for changes in compositional variation among spiders (see Fig. 4a) is caused by the fact that poorly dispersing habitat specialists occur in fewer sites than good dispersers and habitat generalists. This indicates that habitat fragmentation limits the dispersal of these spider species. For vascular plants, we found a trend towards interaction between habitat affinity and dispersal ability with respect to changes in occupancy: characteristic species tended to increase more if they had long-distance dispersal mechanisms, although this effect was not significant ($p = 0.06$). For woodlice we found a strong correlation between occurrence change and body size, which was used as a proxy for dispersal ability. Large bodied species (>10 mm), like *Armadillidium vulgare*, *Porcellio dilatatus*, *Porcellio scaber* and *Trachelipus rathkii* increased in occurrence, while small-bodied species such as *Platyarthrus hoffmannseggi* and *Trichoniscus pusillus* declined. This could indicate that species recovery was limited by habitat isolation and fragmentation. However, no hard conclusions can be drawn from this relationship, as body size is equally related to other responses, including drought or heat resistance (Calder 1984; Peters 1986). Small species tend to be more vulnerable to drought (Kaspari 1993; Kærsgaard et al. 2004; Dias et al. 2012) and heat (Peters 1986) than larger species, presenting an alternative explanation for the observed relationship. The lack of a coherent effect of dispersal ability across taxonomic groups may be caused by the fact that the absolute dispersal ability of 'good' and 'poor' dispersers varies considerably between groups. True bugs classified as 'good dispersers' (i.e. species capable of active flight) are likely to reach much longer distances in a single generation than 'good dispersing' plants, which was defined as those with a long

distance dispersal strategy. Moreover, trait variation within some taxonomic groups may be too small to have an effect.

Overall, the explanatory power of single traits in our study was generally low. This is likely to be partly due to the crude trait categories we adopted, due to a lack of more accurate autecological data for some of the studied taxonomic groups. However, there is also a more fundamental reason for the lack of trait-environment responses. The adaptive value of a specific trait is contingent upon a species' body-plan and its other traits (Verberk et al. 2013). This means that the vulnerability of a species to a specific environmental factor depends on the effect of all its traits combined. More elaborate analyses, incorporating a wide range of traits and explicit trait interactions, e.g. through the use of life-history strategies, are likely to generate better insight (van Noordwijk et al. 2012a; Verberk et al. 2013; van Noordwijk 2014).

## Conclusions and implications

In all, our results indicate that 17 years of conservation management in Dutch calcareous grasslands has not led to the anticipated overall increase in local species richness across all taxonomic groups. However, considering the ongoing biodiversity decline in agricultural landscapes, our results do indicate moderate conservation success (lack of decline among plants, ants, spiders and woodlice, increased richness of millipedes and true bugs and increases in characteristic spiders and weevil food specialists). Local biodiversity conservation seems to have been limited in particular by species' inability to recolonize suitable habitat in this highly fragmented landscape. In addition, the management regime seems to have been insufficient to create favorable habitat conditions for some characteristic species, particularly carabid beetles and weevils. Intensive autumn management in Dutch calcareous grasslands may cause particular obstacles for their larval stages, as was previously demonstrated for ants (van Noordwijk et al. 2012a) and butterflies (van Noordwijk et al. 2012b).

An encouraging result of our study is that local diversity shifts were generally paralleled by shifts in regional diversity and compositional variation in the same direction. Implementation of relatively uniform conservation management at the regional scale, consisting of intensive autumn grazing and/or mowing, did not lead to a uniform change in species composition. This suggests that the management succeeded in maintaining or even enhancing the unique character of each site, attracting different species to different sites. Although this is certainly a positive result, it may in fact partially reflect the high level of fragmentation of the study landscape. If species are only able to recolonize restored sites over short distances, then regional introduction of uniform conservation management is indeed unlikely to lead to biotic homogenization. In addition, the spider data in our study demonstrate that successful management (in terms of increased occurrence of characteristic species) does not always lead to increased compositional variation among sites. Theoretically, successful conservation management can even contribute to biotic homogenization in a positive way, e.g. if it causes characteristic species to be present in all study sites (recall Fig. 1). Therefore, biotic homogenization should not by definition be considered as a process that needs to be avoided and countered. Instead, providing a range of environmental conditions to suit different species is paramount for safeguarding regional biodiversity, irrespective of whether these conditions are present in the same or in separate sites.

In line with earlier studies (Kruess and Tscharntke 2002; Devin et al. 2005; Oertli et al. 2005; Shaw et al. 2010), our results demonstrate that diversity shifts differ markedly

among taxonomic groups. This demonstrates the need to adopt a wide taxonomic scope when evaluating strategies to tackle diversity loss and the need to understand underlying mechanisms. Although the explanatory power of our single trait analyses was generally low, it did shed some light on the mechanisms underlying observed diversity shifts, particularly highlighting dispersal constraints. In addition, we found that holometabolous taxonomic groups declined more than hemimetabolous arthropods. This intriguing observation warrants further investigation.

**Acknowledgements** We thank Natuurmonumenten, Staatsbosbeheer and Stichting het Limburgs Landschap for their kind permission to conduct research on their premises. Many thanks go to Nina Smits and Wim Ozinga for kindly providing the vascular plant data and plant trait data respectively. We are very grateful to Jan Kuper, Remco Versluijs, Theo Peeters, Albert Dees, Stef Waasdorp, Marten Geertsma and Wim Dimmers for their help with data collection and to four anonymous referees for their helpful comments on earlier versions of this manuscript. This research was conducted as part of the chalk grassland Project (projectnr: O + BN/2009/dk 118) within the Development and Management of Nature quality program, financed by the Dutch Ministry of Economy, Agriculture and Innovation. Toos van Noordwijk received financial support from Gent University (BOF, joint PhD grant) and Radboud University Nijmegen.



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